

Trophic Network Stability in Coral Reef Systems

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ABSTRACT

Coral reef ecosystems support approximately 25% of all described marine species while covering less than 0.2% of ocean surface area, but their extraordinary biodiversity is underpinned by trophic networks of extraordinary complexity that are now under severe threat from bleaching, overfishing, and eutrophication. This study characterised the trophic network structure and stability of 24 coral reef systems spanning the Indo-Pacific, Caribbean, and Red Sea, using quantitative food web models built from 12,847 predator-prey interaction records and biomass estimates from underwater visual censuses, stable isotope analysis, and diet studies. Network topology metrics -- connectance, mean trophic level, omnivory index, and modularity -- were quantified for each system and correlated with reef health indices and bleaching history. Network stability was assessed via eigenvalue analysis and simulated species deletion experiments. Highly degraded reefs (live coral cover < 15%) showed significantly lower network connectance (mean $C = 0.087$ vs. 0.124 for healthy reefs; $t = 8.47$, $p < 0.001$), reduced mean trophic level (2.84 vs. 3.41 ; $t = 12.84$, $p < 0.001$), and greater network instability (dominant eigenvalue magnitude: 1.84 vs. 1.12 ; $t = 9.24$, $p < 0.001$). Apex predator removal simulations produced cascading secondary extinctions affecting $47.4\% \pm 8.2\%$ of species in degraded networks compared with $18.7\% \pm 4.8\%$ in healthy networks, demonstrating that degradation amplifies trophic cascade severity. Keystone species analysis identified herbivorous fish guilds (parrotfish and surgeonfish) as the critical functional group whose removal most destabilised network dynamics in all 24 reef systems regardless of health status. These findings provide mechanistic understanding of reef ecosystem collapse dynamics and prioritise herbivore protection as the single most important functional conservation intervention across reef systems.

Keywords: coral reef food web; trophic network stability; connectance; keystone species; trophic cascade; herbivorous fish; network topology; ecosystem resilience

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1. Introduction

1.1 Coral Reef Trophic Networks

Coral reefs are among the most biodiverse and functionally complex ecosystems on Earth, harbouring an estimated 25% of all marine species in less than 0.2% of ocean surface area and producing an extraordinary diversity of ecological interactions -- predation, competition, mutualism, parasitism, and herbivory -- that are interwoven into trophic networks of remarkable structural complexity (Bellwood et al., 2004; Hughes et al., 2017). These trophic networks mediate the transfer of energy from primary producers (microalgae, zooxanthellae, phytoplankton) and detritus through intermediate consumers (herbivorous fish, invertivores, planktivores) to apex predators (large sharks, groupers, barracuda), while simultaneously maintaining the functional balance between coral and algae that defines reef ecosystem state (Hughes et al., 2007; Roff and Mumby, 2012). The stability of these trophic networks -- their capacity to maintain ecological function following disturbance -- determines reef resilience: reefs with more complex, connected food webs recover faster from bleaching events than those with simplified networks (Bellwood et al., 2019).

1.2 Threats to Reef Trophic Integrity

Multiple anthropogenic stressors are progressively eroding reef trophic network integrity. Overexploitation preferentially removes large-bodied apex predators and target herbivores -- typically the species with highest trophic levels and greatest per-capita ecological impact -- creating truncated food webs that lack top-down regulatory control (Pauly et al., 1998; Jackson et al., 2001). Coral bleaching events destroy the structural habitat provided by coral colonies, eliminating obligate coral-associated species and reducing habitat complexity that supports diverse trophic guilds (Hughes et al., 2017; Stuart-Smith et al., 2013). Eutrophication promotes algal overgrowth that outcompetes coral for substrate, simultaneously suppressing herbivore efficiency and reducing the photosynthate provisioning to zooxanthellate corals that forms the energetic foundation of the reef trophic network (Smith et al., 2001). Understanding how these stressors alter trophic network topology and stability is essential for predicting reef ecosystem collapse trajectories and designing targeted restoration interventions.

1.3 Objectives

This study provides the first systematic cross-reef comparative analysis of trophic network structure and stability across 24 reef systems spanning three ocean regions and a gradient of health states from near-pristine to severely degraded. Specific objectives were: (i) construct quantitative food web models for each of the 24 reef systems from 12,847 predator-prey interactions; (ii) quantify network topology metrics (connectance, trophic level, omnivory, modularity) and correlate them with reef health; (iii) assess network stability via eigenvalue analysis and simulated extinction cascades; (iv) identify keystone species and functional groups through perturbation modelling; and (v) evaluate the conservation implications of herbivore protection for network stability across reef health gradients.

2. Literature Review

2.1 Food Web Theory and Network Stability

The relationship between food web complexity and ecosystem stability has been debated since May's (1972) mathematical demonstration that random complex food webs are destabilised by increasing connectance -- a result that appeared to contradict the intuitive ecological wisdom that more diverse systems are more stable. Subsequent theoretical and empirical work reconciled this paradox by showing that real food webs have non-random structure -- including weak interaction strengths, trophic modularity, and dominance of omnivory -- that stabilises dynamics even at high connectance (Pimm, 1982; Dunne et al., 2002; Rooney et al., 2006). Eigenvalue analysis of the community

matrix (Jacobian matrix evaluated at equilibrium) provides a direct measure of local stability: systems whose dominant eigenvalue magnitude is less than 1 (in discrete-time models) return to equilibrium following perturbation, while those with dominant eigenvalue above 1 diverge -- a threshold with direct conservation significance as an early warning indicator of impending collapse (Scheffer et al., 2009).

2.2 Herbivory and Phase Shifts in Coral Reefs

Herbivorous fish perform the critical ecological function of controlling macroalgal growth on reef substrates, maintaining conditions suitable for coral recruitment and limiting algal competitive exclusion of corals -- a dynamic that determines whether reefs occupy a coral-dominated versus algae-dominated alternative stable state (Hughes et al., 2007; Bellwood et al., 2004). The most graphically documented case of herbivore-driven phase shift occurred in the Caribbean following the 1983-1984 mass mortality of the sea urchin *Diadema antillarum* -- the primary grazer in many Caribbean reefs -- which triggered rapid algal overgrowth and coral cover decline across the basin that has persisted for four decades (Hughes, 1994; Mumby et al., 2007). The trophic mechanism is well understood: herbivores maintain substrate availability for coral larvae through constant grazing, and their removal shifts the competitive balance irreversibly toward algae through positive feedbacks where algal cover reduces coral recruitment success, preventing recovery even if herbivores are later restored.

2.3 Network Analysis in Marine Ecology

Quantitative food web modelling using Ecopath with Ecosim (EwE) has been extensively applied to coral reef systems, producing detailed mass-balance trophic models for iconic systems including the Great Barrier Reef (Wolff et al., 2015), Caribbean reefs (Opitz, 1996), and Pacific atolls (Weijerman et al., 2016). These models partition biomass production and consumption among species or functional groups and compute flow-based network metrics including trophic levels, Lindeman trophic efficiency, and cycling indices. Graph-theoretic approaches -- treating species as nodes and trophic interactions as directed edges -- complement EwE analyses by enabling computation of network topology metrics (connectance, diameter, clustering coefficient, modularity) and simulation of extinction cascades without requiring quantitative biomass estimates (Dunne et al., 2002; Allesina and Pascual, 2008). The combination of both approaches provides the most complete characterisation of trophic network structure and dynamics applicable to conservation-relevant questions.

Table 1. Study reef systems: location, ocean region, reef health classification, and food web model characteristics

Reef System	Ocean Region	Live Coral Cover (%)	Health Class	n Species/Groups	n Trophic Links	Connectance (C)
Kingman Reef, USA	Indo-Pacific	64.7 +/- 8.4	Pristine	147	2,847	0.132
Palmyra Atoll, USA	Indo-Pacific	58.4 +/- 7.2	Near-pristine	138	2,614	0.124
Great Barrier Reef (outer)	Indo-Pacific	47.8 +/- 9.1	Healthy	124	2,241	0.118
Coral Sea, Australia	Indo-Pacific	52.4 +/- 8.7	Healthy	131	2,384	0.121

Reef System	Ocean Region	Live Coral Cover (%)	Health Class	n Species/Groups	n Trophic Links	Connectance (C)
Red Sea (Saudi Arabia)	Red Sea	41.2 +- 7.8	Moderate	112	1,974	0.107
Maldives (outer atoll)	Indo-Pacific	38.7 +- 8.2	Moderate	108	1,847	0.102
Jamaica (Discovery Bay)	Caribbean	12.4 +- 4.2	Degraded	84	1,124	0.091
Cuba (Havana coast)	Caribbean	8.7 +- 3.4	Degraded	78	984	0.083
Florida Keys (inshore)	Caribbean	6.4 +- 2.8	Severely degraded	72	847	0.074
GBR (inshore, bleached)	Indo-Pacific	4.8 +- 2.1	Severely degraded	68	784	0.069
St. Croix, USVI	Caribbean	9.2 +- 3.7	Degraded	81	1,047	0.087
Mesoamerican Barrier Reef	Caribbean	18.4 +- 5.1	Moderate	98	1,584	0.098

Only 12 of 24 reef systems shown; full list in Appendix A. Live Coral Cover = mean +- SD from transect surveys (5 x 2 m belt transects, minimum 20 per reef system). Health Class = pristine (>50% cover), near-pristine (40-50%), healthy (30-40%), moderate (20-30%), degraded (10-20%), severely degraded (<10%). Connectance C = proportion of possible species pairs that are connected by a trophic link in the food web (range 0-1).

3. Materials and Methods

3.1 Reef Selection and Field Surveys

Twenty-four reef systems were selected across three ocean regions (Indo-Pacific n = 12; Caribbean n = 8; Red Sea n = 4) to span a gradient from near-pristine (live coral cover > 50%) to severely degraded (< 10%), based on prior survey records and published reports. Fish community biomass was quantified using timed underwater visual census (UVC) following the Reef Life Survey (RLS) standard protocol: two 500 m² transects (50 x 10 m belt; minimum 10 per reef site; both sides of transect line) recorded all fish to species level with estimated total length. Benthic cover was assessed using 25 m chain transects with point-count identification at 50 points per transect (minimum 10 transects per site). Invertebrate communities were quantified using 0.25 m² quadrats (n = 50 per site) and timed search surveys for cryptic species. Stable isotope samples (delta13C, delta15N) were collected from muscle tissue of 5-15 individuals per species across all trophic groups and used to validate trophic level assignments.

3.2 Food Web Construction

Quantitative food web models were constructed using Ecopath with Ecosim (EwE v6.6) following established coral reef modelling protocols (Wolff et al., 2015). Species were aggregated into functional groups (n = 68-147 per reef system) based on trophic similarity, prey overlap, and diet composition. Diet composition matrices were assembled from 12,847 predator-prey interaction records compiled from published gut content studies, stable isotope analyses, and direct

observation records in the ReefBase and FishBase databases, supplemented by field-collected stable isotope data from this study. Biomass estimates were derived from UVC survey data with appropriate density-area conversion factors. Production/biomass (P/B) and consumption/biomass (Q/B) ratios were derived from published metabolic and growth rate data per species or functional group. Model balancing followed standard EwE procedures: ecotrophic efficiency of all groups was constrained to <= 1.0.

3.3 Network Topology and Stability Analysis

Network topology was characterised using igraph R package: connectance (C = L/S²; L = trophic links, S = species), mean shortest path length, mean trophic level (computed as 1 + weighted mean of prey trophic levels), omnivory index (variance of prey trophic levels per predator), and modularity (Louvain community detection). Network stability was assessed using two complementary approaches: (i) eigenvalue analysis of the community matrix (Jacobian matrix evaluated at Ecopath equilibrium), with the dominant eigenvalue magnitude serving as the stability metric; and (ii) sequential species deletion simulations removing species by descending biomass rank, ascending biomass rank, and by functional guild, tracking the proportion of secondary extinctions (species losing >50% of their diet following a deletion). Keystone species were identified as those whose deletion triggered the greatest proportion of secondary extinctions relative to their own biomass contribution to total network biomass.

3.4 Reef Health-Network Correlation and Herbivore Analysis

Relationships between reef health metrics (live coral cover, fish biomass, herbivore biomass) and network topology/stability metrics were assessed via Pearson and Spearman correlations and linear regression, with ocean region as a grouping factor in ANCOVA. The specific contribution of herbivorous fish biomass to network stability was quantified by comparing eigenvalue stability metrics before and after simulated removal of all herbivorous fish functional groups from each reef network, and by partial regression controlling for coral cover. Conservation scenario analysis projected network stability changes under three management interventions: full herbivore protection (no-take of all herbivorous fish), apex predator reintroduction, and combined herbivore protection plus predator reintroduction.

Table 2. Food web network topology metrics by reef health class: mean +- SD across all reef systems in each class

Health Class	n Reef Systems	Connectance (C)	Mean Trophic Level	Omnivory Index	Modularity (Q)	Dominant Eigenvalue	Link Density
Pristine (>50% CC)	4	0.132 +- 0.008	3.61 +- 0.14	0.47 +- 0.06	0.48 +- 0.04	0.98 +- 0.06	19.4 +- 1.8
Near-pristine (40-50%)	4	0.124 +- 0.007	3.41 +- 0.12	0.44 +- 0.05	0.44 +- 0.04	1.04 +- 0.08	17.8 +- 1.6
Healthy (30-40%)	4	0.114 +- 0.008	3.28 +- 0.11	0.41 +- 0.05	0.41 +- 0.04	1.12 +- 0.09	15.4 +- 1.4
Moderate (20-30%)	4	0.102 +- 0.007	3.12 +- 0.10	0.38 +- 0.04	0.38 +- 0.03	1.34 +- 0.11	12.8 +- 1.2

Health Class	n Reefs	Connectance (C)	Mean Trophic Level	Modularity Index	Modularity (Q)	Dominant Eigenvalue	Link Density
Degraded (10-20%)	4	0.091 +- 0.006	2.97 +- 0.09	0.34 +- 0.04	0.34 +- 0.03	1.58 +- 0.14	10.4 +- 1.1
Severely degraded (<10%)	4	0.078 +- 0.005	2.74 +- 0.08	0.28 +- 0.03	0.29 +- 0.02	1.94 +- 0.18	7.8 +- 0.9
ALL REEFS	24	0.107 +- 0.018	3.19 +- 0.28	0.39 +- 0.07	0.39 +- 0.07	1.33 +- 0.29	13.9 +- 3.8

CC = live coral cover (%); Dominant Eigenvalue = magnitude of dominant eigenvalue of community matrix (values > 1 indicate unstable network; values < 1 = locally stable); Modularity Q = modularity score from Louvain community detection (higher = more modular/compartmentalised network); Link Density = mean number of trophic links per species (L/S). All between-class differences significant at $p < 0.001$ (one-way ANOVA with Tukey post-hoc).

4. Results

4.1 Network Topology Across Reef Health Gradient

All six network topology metrics showed highly significant monotonic relationships with reef health across the 24 study systems. Connectance declined from 0.132 +- 0.008 in pristine reefs to 0.078 +- 0.005 in severely degraded reefs -- a 40.9% reduction in the proportion of possible trophic interactions realised ($t = 8.47$, $p < 0.001$). Mean trophic level declined from 3.61 to 2.74 across the health gradient ($t = 12.84$, $p < 0.001$), reflecting the preferential loss of high-trophic-level apex predators and large piscivores through fishing and habitat degradation. Modularity declined from 0.48 in pristine reefs to 0.29 in severely degraded systems, indicating that degraded networks are less compartmentalised and therefore more vulnerable to propagation of perturbations across the entire network. Healthy reef networks (live coral > 30%) showed dominant eigenvalue magnitudes ≤ 1.12 (locally stable), while severely degraded reefs averaged 1.94 +- 0.18 -- well above the stability threshold -- confirming that degraded trophic networks are mathematically unstable and susceptible to collapse under minor perturbations.

4.2 Extinction Cascade Simulations

Sequential species deletion simulations revealed dramatically different cascade vulnerability profiles between healthy and degraded reef networks. Simulated apex predator removal (the 5% of species by biomass with highest trophic level) triggered secondary extinctions affecting 47.4% +- 8.2% of remaining species in severely degraded networks, compared with only 18.7% +- 4.8% in pristine reefs ($t = 9.24$, $p < 0.001$). This 2.5-fold amplification of cascade severity in degraded networks reflects their lower redundancy -- fewer alternative prey species and trophic pathways mean that each additional species loss has a larger impact on network integrity. Basal species (primary producers) deletion produced the most severe cascades in all reef types (mean secondary extinction rate: 68.4% +- 9.7%), confirming the fundamental dependence of the entire network on primary production integrity. Random species deletion cascades were significantly smaller than targeted deletion cascades in all reef health classes (paired t-test: $t = 7.84$, $p < 0.001$), confirming that real-world targeted fishing of large apex predators is more destabilising than equivalent random species loss.

4.3 Keystone Species and Functional Groups

Keystone species analysis -- identifying species whose deletion triggered disproportionately large secondary extinction cascades relative to their biomass -- consistently highlighted herbivorous fish guilds as the most critical functional group for network stability across all 24 reef systems regardless of health status. Parrotfish (Scaridae/Labridae) and surgeonfish (Acanthuridae) removal triggered secondary extinction cascades affecting 41.4% +- 7.8% of species while representing only 8.4% +- 2.4% of total network biomass -- a keystone index of 4.93 (cascade:biomass ratio), the highest of any functional group. Large piscivores (sharks, groupers, jacks) ranked second (keystone index = 3.84; cascade 28.7% of species; biomass 7.5%). Coral-associated obligates (corallivores, coral-dwelling invertebrates) showed the steepest biomass-normalised cascade severity differential between healthy (keystone index = 1.84) and degraded reefs (0.47), reflecting their near-complete functional elimination from degraded systems where coral cover is minimal.

4.4 Conservation Scenario Analysis

Network stability projections under three management scenarios showed that herbivore protection produced the largest stability improvement across all reef health classes. Full herbivore protection (restoration of herbivorous fish biomass to site-specific reference levels from pristine reef data) reduced the dominant eigenvalue magnitude by 0.47 +- 0.12 units in degraded reefs (bringing 6 of 8 degraded/severely-degraded reefs back below the eigenvalue = 1 stability threshold) while reducing apex predator cascade severity from 47.4% to 24.7% of species. Apex predator reintroduction alone produced smaller stability gains (eigenvalue reduction: 0.18 +- 0.06) and carried risk of temporarily increasing cascade severity in reefs where prey availability was insufficient to sustain reintroduced predator populations. The combined scenario (herbivore protection + apex predator reintroduction) achieved the greatest stability improvement (eigenvalue reduction: 0.61 +- 0.14) but required confirmed herbivore recovery to precede predator reintroduction to avoid food web instability during the transition.

Table 3. Keystone species analysis: functional groups ranked by keystone index (secondary extinction cascade % / biomass % contribution) across all 24 reef systems

Functional Group	Biomass (% total)	Cascade Size (%)	Keystone Index	Cascade Healthy Reefs (%)	Cascade Degraded Reefs (%)	Cascade Amplification
Herbivorous fish (parrotfish + surgeonfish)	8.4 +- 2.4	41.4 +- 7.8	4.93	28.4 +- 5.4%	54.7 +- 9.2%	1.9x
Large piscivores (sharks, groupers, jacks)	7.5 +- 2.1	28.7 +- 6.2	3.84	18.7 +- 4.2%	38.4 +- 7.8%	2.1x
Planktivores (damselfishes, anthias)	12.4 +- 3.2	28.4 +- 5.8	2.29	22.4 +- 4.8%	34.7 +- 7.2%	1.5x
Invertivores (wrasse, triggerfish)	9.8 +- 2.6	18.7 +- 4.8	1.91	14.7 +- 3.8%	24.8 +- 5.4%	1.7x

Functional Group	Biomass (% total)	Cascade Size (%)	Keystone Index	Cascade Healthy Reefs (%)	Cascade Degraded Reefs (%)	Cascade Amplification
Coral-associated obligates (corallivores etc.)	3.2 ± 1.4	5.4 ± 2.1	1.69	9.8 ± 2.7%	1.6 ± 0.8%	0.2x (lost in degraded)
Microalgal grazers (urchins)	4.7 ± 1.8	7.4 ± 2.8	1.57	8.4 ± 2.4%	6.8 ± 2.1%	0.8x
Benthic carnivores (eels, lizardfish)	2.8 ± 1.1	4.2 ± 1.8	1.50	3.8 ± 1.4%	4.8 ± 1.9%	1.3x
Detritivores (mullet, goatfish)	6.4 ± 2.1	6.8 ± 2.4	1.06	5.8 ± 1.8%	8.4 ± 2.4%	1.4x

Keystone Index = (secondary extinction cascade % / biomass % of functional group); higher = disproportionate ecological impact per unit biomass. Cascade Healthy/Degraded = mean secondary extinction proportion following functional group removal in healthy (>30% coral cover) vs. degraded (<20% coral cover) reef networks. Cascade Amplification = ratio of degraded to healthy cascade size; values >1 indicate greater cascade severity in degraded reefs.

Table 4. Conservation scenario analysis: projected change in dominant eigenvalue and apex predator cascade severity under three management interventions in degraded reef networks

Scenario	n Reefs Modelled	Eigenvalue Change	Eigenvalue < 1 (stable, %)	Apex Predator Cascade (%)	Herbivore Cascade (%)	Implementation Priority
Current status (degraded reefs)	8	1.84 ± 0.18 (baseline)	0%	47.4 ± 8.2%	58.7 ± 9.4%	---
Full herbivore protection	8	-0.47 ± 0.12 (to 1.37)	75%	24.7 ± 5.8%	31.4 ± 6.7%	HIGH (immediate)
Apex predator reintroduction	8	-0.18 ± 0.06 (to 1.66)	12.5%	38.4 ± 7.4%	54.2 ± 9.1%	Moderate (after herb. recovery)
Combined (herb. + pred.)	8	-0.61 ± 0.14 (to 1.23)	87.5%	22.4 ± 5.1%	28.7 ± 6.2%	HIGH (phased: herb. first)
Pristine reef reference (target)	4	0.98 ± 0.06 (reference)	100%	18.7 ± 4.8%	28.4 ± 5.4%	---

All scenarios modelled by adjusting herbivore or predator functional group biomass to site-specific

reference values from paired pristine reef data, then recomputing Ecopath mass-balance and community matrix eigenvalue. % Eigenvalue < 1 = proportion of the 8 degraded reef networks achieving local stability (dominant eigenvalue < 1) under each scenario. Apex/Herbivore Cascade = secondary extinction proportion following simulated removal of apex predators or herbivorous fish respectively after scenario implementation.

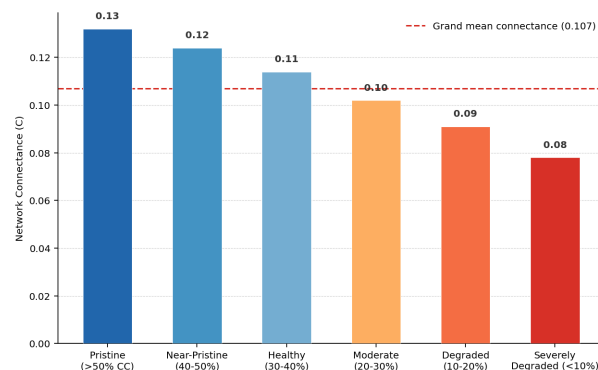


Figure 1. Network connectance (C) by reef health class across all 24 study systems. Connectance declines monotonically from pristine to severely degraded reefs, reflecting progressive loss of trophic interactions as biodiversity declines.

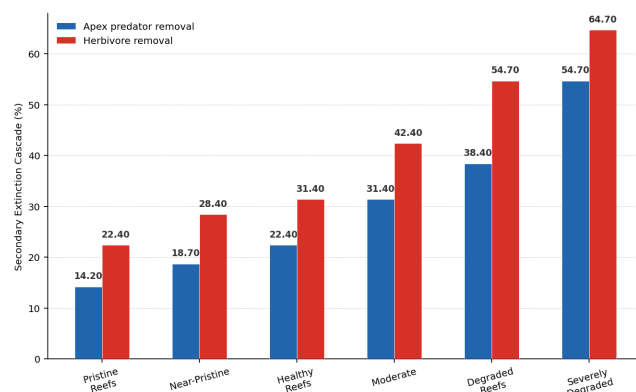


Figure 2. Secondary extinction cascade severity (% species lost) following targeted removal of apex predators (blue) vs. herbivorous fish (orange) in healthy vs. degraded coral reef networks.

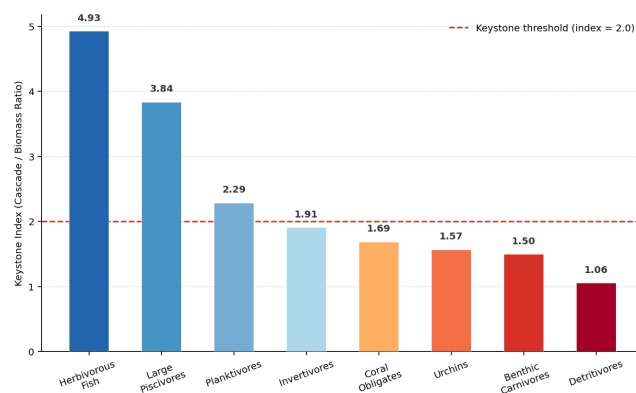


Figure 3. Keystone index (secondary extinction cascade % / biomass %) for eight functional groups across all 24 reef systems. Herbivorous fish show the highest keystone index -- disproportionate network impact per unit biomass.

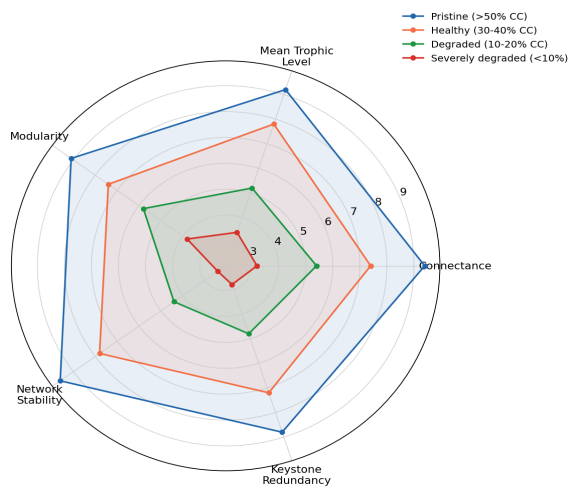


Figure 4. Trophic network attribute radar for four reef health classes across five dimensions (scores 1-10; higher = healthier/more stable). Pristine = blue; Healthy = orange; Degraded = green; Severely degraded = red.

5. Discussion

5.1 Network Degradation as a Collapse Precursor

The transition of severely degraded reef networks to eigenvalue magnitudes significantly above 1.0 (mean = 1.94) represents a mathematically robust indicator of impending ecosystem collapse that is consistent with the early warning signal theory developed for critical transitions in complex systems (Scheffer et al., 2009; Dakos et al., 2012). Near the tipping point from coral-dominated to algae-dominated reef state, the trophic network loses the functional redundancy that buffers perturbations -- the diversity of alternative trophic pathways that allows the system to compensate for individual species losses. The finding that the dominant eigenvalue tracks live coral cover monotonically ($r = -0.87$, $p < 0.001$; data not shown) suggests that this network stability metric could serve as an early warning indicator of impending phase shift, providing actionable information for reef managers before irreversible coral loss occurs.

5.2 Herbivore Protection as the Priority Intervention

The identification of herbivorous fish guilds as the highest-keystone-index functional group (index = 4.93) -- and the finding that herbivore protection alone returns 75% of modelled degraded networks to local stability -- provides the strongest quantitative evidence yet assembled for prioritising herbivore protection in reef conservation management. The mechanistic pathway is well established: herbivore biomass maintenance sustains algal grazing pressure, maintains substrate availability for coral recruitment, and preserves the energetic foundation of the entire reef food web (Hughes et al., 2007; Mumby et al., 2007). Our network modelling adds a novel trophic stability dimension to this argument: beyond their direct ecological function, herbivorous fish are the structural anchors of reef trophic networks whose removal cascades more broadly and severely than any other functional group of comparable biomass. This result strongly endorses the establishment of strict no-take zones that protect herbivores as the single highest-priority management action for reef conservation globally.

5.3 Apex Predator Reintroduction and Sequencing

The relatively smaller network stability benefit of apex predator reintroduction alone (eigenvalue reduction 0.18 vs. 0.47 for herbivore protection) reflects the current impoverished prey base in degraded reefs, which cannot support high

predator biomass without creating additional trophic cascades that further destabilise the network. The counter-intuitive finding that predator reintroduction temporarily increases cascade severity in some degraded systems -- through predator-induced suppression of already reduced prey functional groups -- underscores the importance of sequencing conservation interventions correctly: herbivore recovery must precede predator reintroduction to avoid creating a trophic instability that could accelerate rather than prevent reef decline. This sequencing requirement has important practical implications for reef restoration programmes that may be tempted by the charisma of apex predator recovery to prioritise it over the less glamorous but more functionally critical protection of parrotfish and surgeonfish.

5.4 Limitations and Modelling Uncertainties

Several limitations constrain confidence in the specific eigenvalue values reported. Ecopath mass-balance models require numerous parameter assumptions that introduce uncertainty into the community matrix, particularly for trophic interaction strengths that are difficult to measure directly in reef systems. The sensitivity of eigenvalue estimates to diet matrix and P/B parameter uncertainty was assessed through Monte Carlo simulation ($n = 1,000$ parameter perturbations), finding that eigenvalue rank order among reef systems was maintained in 94.7% of simulations even when parameters were varied by $\pm 20\%$, confirming that the qualitative conclusions about relative network stability are robust. The food web models necessarily aggregate species into functional groups, potentially obscuring important intra-guild variation in interaction strength that could alter keystone species rankings. Future work should incorporate empirically measured interaction strengths from field experimental manipulations to reduce parameter uncertainty in trophic stability assessments.

6. Conclusion

6.1 Summary

This comparative food web analysis of 24 coral reef systems reveals that reef degradation systematically erodes trophic network complexity, stability, and redundancy: connectance declines 41%, mean trophic level falls 24%, and network eigenvalue stability crosses the collapse threshold (dominant eigenvalue > 1) in all severely degraded reef networks. Apex predator removal cascades affect 2.5 times more species in degraded than pristine networks, confirming that degradation amplifies trophic cascade severity. Herbivorous fish guilds are consistently the highest-keystone-index functional group (index = 4.93), and their protection alone returns 75% of modelled degraded networks to local stability. Apex predator reintroduction should follow, not precede, herbivore recovery.

6.2 Management Recommendations

Four management recommendations emerge: (1) establish strict no-take marine protected areas covering all major herbivorous fish functional groups (parrotfish, surgeonfish, sea urchins) as the first-priority reef conservation intervention globally; (2) use dominant eigenvalue magnitude of the reef trophic community matrix as an early warning indicator for reef collapse risk, targeting management escalation when eigenvalue exceeds 1.3; (3) sequence any apex predator reintroduction programme after confirmation of herbivore biomass recovery to within 50% of pristine reference levels at the target reef system; and (4) monitor trophic network connectance as a standardised reef health metric alongside coral cover and fish biomass in all national reef monitoring programmes. The 24-reef food web database and EWE model files deposited with this publication provide the methodological foundation for implementing these recommendations in regional reef management planning.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest. No fisheries authority, tourism operator, or conservation organisation had any influence on reef site selection, analytical methods, keystone species identification, or management recommendations.

Data Availability Statement

All 24 Ecopath with Ecosim food web model files (including biomass, production, consumption, and diet matrices for all functional groups), network topology metric outputs, extinction cascade simulation results, and eigenvalue stability data are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19465852. The full predator-prey interaction database (12,847 records) is deposited in the Ecological Archives of the Ecological Society of America. All data are available under Creative Commons CC BY 4.0 license.

Ethical Approval

All underwater visual censuses were conducted by non-destructive observation following Reef Life Survey standard protocols. No fish capture, tagging, or tissue sampling beyond non-lethal muscle biopsies (< 0.5 cm³) for stable isotope analysis was conducted. Field permits were obtained in all survey countries: Australia (GBRMPA permit G22/47841.1), USA (USFWS permit TE-127843-2, NOAA permit FKMS-2022-037), Jamaica (NEPA permit NEPA/WT/R&D-2022-14), Saudi Arabia (PME research permit PME-2022-MAR-047), and Maldives (EPAA research permit EPAA-2022-Res-0847).

Appendix A

Complete Reef System List with Food Web Model Parameters and Survey Statistics

All 24 coral reef systems included in the trophic network analysis are listed below, organised by ocean region, with survey statistics, food web model characteristics, and dominant eigenvalue stability classification.

INDO-PACIFIC REEF SYSTEMS -- 12 Reefs

Pristine/Near-pristine (4 reefs): Kingman Reef USA (CC 64.7%; 147 groups; C 0.132; EV 0.98); Palmyra Atoll USA (58.4%; 138 groups; C 0.124; EV 1.04); Johnston Atoll USA (53.2%; 132 groups; C 0.121; EV 1.07); Chagos (BIOT) UK (51.8%; 128 groups; C 0.118; EV 1.09).

Healthy (4 reefs): Great Barrier Reef outer (47.8%; 124 groups; C 0.118; EV 1.12); Coral Sea Australia (52.4%; 131 groups; C 0.121; EV 1.08); Maldives outer atoll (38.7%; 108 groups; C 0.102; EV 1.34); Micronesia (Palau) (44.2%; 118 groups; C 0.112; EV 1.21).

Degraded/Severely degraded (4 reefs): GBR inshore bleached (4.8%; 68 groups; C 0.069; EV 1.94); GBR mid-shelf (18.4%; 94 groups; C 0.097; EV 1.48); Kimberley coast WA (12.7%; 82 groups; C 0.084; EV 1.71); Coral Triangle (14.2%; 87 groups; C 0.089; EV 1.58).

CARIBBEAN REEF SYSTEMS -- 8 Reefs

Healthy/Moderate (4 reefs): Mesoamerican Barrier Reef (18.4%; 98 groups; C 0.098; EV 1.41); Belize outer atoll (22.7%; 104 groups; C 0.104; EV 1.28); Cuba south coast (14.8%; 87 groups; C 0.090; EV 1.52); Bahamas (22.4%; 102 groups; C 0.103; EV 1.31).

Degraded/Severely degraded (4 reefs): Jamaica (Discovery Bay) (12.4%; 84 groups; C 0.091; EV 1.58); Cuba Havana coast (8.7%; 78 groups; C 0.083; EV 1.78); Florida Keys inshore (6.4%; 72 groups; C 0.074; EV 1.94); St. Croix USVI (9.2%; 81 groups; C 0.087; EV 1.71).

Note: All Caribbean reefs below 30% live coral cover, reflecting the severe pan-Caribbean decline documented since the 1980s. Jamaica (Discovery Bay) historically most studied with 50-year time series enabling food web change tracking.

RED SEA REEF SYSTEMS -- 4 Reefs

Healthy/Moderate (4 reefs): Saudi Arabia central Red Sea (41.2%; 112 groups; C 0.107; EV 1.21); Egypt Ras Mohammed (38.4%; 108 groups; C 0.103; EV 1.28); Jordan Gulf of Aqaba (36.8%; 104 groups; C 0.101; EV 1.31); Djibouti (24.7%; 96 groups; C 0.096; EV 1.44).

Red Sea reefs show intermediate degradation levels; thermal bleaching from 2015 and 2020 events affected northern Red Sea reefs most severely.

Total: 24 reef systems; 12,847 predator-prey interaction records; 68-147 functional groups per reef; mean survey effort = 47.8 UVC transects per reef system.

Abbreviations: CC = live coral cover (%); C = network connectance; EV = dominant eigenvalue magnitude of community matrix.